# BIOLOGY, MORPHOLOGY, AND CYTOPLASMIC STRUCTURE OF ALEURODISCUS

Harvey E. Stork

## Biology of Aleurodiscus amorphus

The results here reported are the outcome of observation and succeeding laboratory study of *Aleurodiscus amorphus* (Pers.) Rabenhorst as found on the balsam fir in the Adirondack Mountains, vicinity of Seventh Lake, Hamilton County, N. Y. This plant has been described under a number of different names, a fact due, in part, to its pezizoid form. Persoon first described it as *Peziza amorpha*. Fries made it a Thelephora and later a Corticium. Quelet put it into the genus Cyphella, and more recently Peck described plants from the Adirondack region as the type of a new genus Nodularia. The plant has characteristic moniliform paraphyses that give a suggestion of an ascus with large spores when examined under low magnification, and this has been one of the misleading characters. In dried plants, too, the contents of the basidia often round up into globular masses which have been mistaken for ascospores.

This Aleurodiscus bears the distinction of being the first Basidiomycete in which a nucleus was definitely described, De Bary (7) having reported and figured in 1866 the fusion nucleus in the basidium. It is not surprising that this should have come to his attention, for the mature basidia are very large, reaching the size of $150 \times 24\ \mu$; and the fusion nucleus (reaching $15\ \mu$) is the largest that the writer has seen in the fungi or of which he finds report in the literature, if the peculiar nucleus of the chytrids be excepted. It was for this reason that the late Professor G. F. Atkinson suggested this plant to the writer in 1915 as a good object for cytological study. Because of the large size of the nuclei, especially in the large basidia, it has been found a most favorable object for the study of nuclear fusion and of the behavior of the elements of the nucleus in karyokinesis. The study of this phase of the subject is, however, incomplete in some of the stages, and a discussion of the details of karyokinesis is left for a subsequent paper, the cytological part of the present study being limited to cytoplasmic structures.

Another species of Aleurodiscus that resembles in many respects the one here discussed is *A. Oakesii*, commonly found on the bark of living Ostrya and less frequently on the bark of several other frondose trees. This species is also being studied by way of comparison with *A. amorphus*. Their fruit bodies are somewhat similar, but they are never found on the same hosts. The fruit bodies of *A. Oakesii* (upper and middle figures, Plate XXXI) are normally more or less cup-shaped, while those of *A.*

*amorphus* (lower figure, Plate XXXI) are normally convex. Those of the former species also tend to be larger and more subject to confluence. Fries (8) considered the two species identical, and more recently Morgan (18) made *A. Oakesii* the same as *A. amorphus*. The character of the paraphyses of the two is, however, quite different, those of *A. amorphus* being moniliform and those of the other species of a peculiar bottle-brush type. These differences were pointed out by Cooke (4) and later by Peirce (19).

The fruit bodies of *A. amorphus* develop during the summer on the surface of twigs and small branches of fallen *Abies balsamea*. They have never been observed on branches larger than three centimeters in diameter. They do not occur on the twigs and branches of living trees, nor on those of trees that have been dead for too long a time. The fungus seems to be definitely selective in the degree of decay of its substratum. During the observation of each of the four summers, the numerous balsam firs that had been blown down by the wind since the preceding summer were never seen to harbor the fungus. But during the second summer after the falling of the tree, the fungus was seen to produce its orange-yellow fruit bodies abundantly, and they might recur in the third summer, but in the fourth summer in the history of a fallen tree no evidence of the life of the fungus was ever observed. In two relatively low fern swamps kept under observation, in which there were numerous balsam firs, some of which were uprooted by the wind each year, one could predict almost with certainty upon which of the fallen trees *A. amorphus* could be found during any one summer. Aside from the balsam fir several other conifers are reported as harboring the fungus as a bark saprophyte, *viz.*, *Abies concolor*, *Thuja plicata*, *Picea* sp., *Tsuga* sp.

The fruit bodies usually are very abundant on the lower and moister sides of twigs and branches and are seldom seen on the upper sides unless these are very well protected from dessication. The habit photographs (Plate XXXI) were made by pointing the camera upward under fallen trees. In descriptions of this species as well as of others of the genus the statement is often made that the fruit bodies are incrusted with mineral matter to such a degree as to make structural studies difficult. In all material used by the writer no incrustations were ever observed, and mineral crystals among the hyphae have never interfered with the making of sections.

A description of the species will not be repeated here. The reader is referred to the description given by Burt (3). A feature not noted in any descriptions is that the mature spores in mass present a distinctly pink tinge, although by transmitted light the spore coat appears hyaline. Hennings (11) describes the color of the hymenium as being at first scarlet, then becoming paler. No material has ever been collected by the writer that had any suggestion of red. The fruit bodies are at first of a yellowish-orange color that may later become paler and even a light buff. The plant no doubt varies in different localities in some of its characters, as is also indicated by Burt's report that, in collections from Idaho westward, the echinulate marking of the spores is very faint.

Another saprophyte of the balsam tree that in the form of its fruit body bears a superficial resemblance to Aleurodiscus is *Dasyscypha Agassizii* (Berk. & Curt.) Sacc. The two are often found side by side, and they are the first two conspicuous saprophytes that attack the tree. After two or three years, when the bark of the twigs becomes somewhat loose from decay, numerous other saprophytes are encountered, most common of which are *Polystictus hirsutus* (Wulf.) Fr., *P. pergamenus* Fr., *Lenzites betulina* (L.) Fr., *Panus stypticus* (Bull.) Fr., *Creonectria cucurbitula* (Sacc.) Seaver, and *Poria* sp.

Aside from the plants above mentioned, the writer has very frequently encountered a small species of Tremella that grows upon the fruit bodies of the Aleurodiscus. Indeed, in more than half the cases in which the latter were found on fallen balsam trees, the Tremella was present. It appears in the form of hyaline glistening droplets on the fruit bodies of the Aleurodiscus, varying in size from microscopic bodies to forms that completely cover the surface of the plant. Cross sections of such fruit bodies harboring the Tremella are shown in figures 9 to 11, Plate XXXII. So far as the writer knows, the plant is truly parasitic and is confined to this host. It was never seen growing on the bark of the balsam fir away from the Aleurodiscus, nor on the other fungi mentioned above as commonly encountered by the side of this one. The Tremella hyphae grow down into the hymenium and subhymenial tissue of the Aleurodiscus and mingle intimately with those of the latter. Beneath the parasite the hyphae of the Aleurodiscus soon cease active growth and for a long time remain in a degenerating condition before they are killed. It is in this condition that the nucleus shows characteristic structures and the cytoplasmic granules undergo significant changes that are to be discussed in detail later.

The writer is unable to identify the Tremella with any species previously described. The species that perhaps approaches it most nearly is *Tremella versicolor* Berk., which was described in Europe as "parasitic on *Corticium nudum* on decorticated trees" (Berkeley, 2). This plant, however, is described as orange in color, at length assuming a rufous tinge, while the one here in question is always hyaline, never assuming even the color of its host. The fruit body consists of an interwoven mass of much branched slender hyphae ($2\frac{1}{2}\ \mu$) which secrete a viscid material that gives the whole a gelatinous consistency. When young, and even at the very beginning of its growth, its surface is usually covered with abundantly branched conidiophores. The conidia are elliptical in shape, $5 \times 7\ \mu$, and stain very densely with safranin or haematoxylin. Large numbers of them are often seen embedded within the lower parts of the older tissue. A very definite hymenium is formed of the globose basidia that divide in the cruciate manner characteristic of the Tremellales. This hymenium stands out in the photomicrograph (fig. 10), the black dots representing basidia. As the sterigmata grow from the four cells of a basidium, the cells split apart to some extent downward. The globose basidia measure 15 μ in diameter when mature, and the sterigmata are slender like the hyphae of the plant and attain a length (up to 30 μ) that gives them the general appearance of germ tubes rather than of sterigmata. It was suggested that the Tremella be described as a new species, but the characteristics that are really distinguishing are so few in this group that it is perhaps better not to multiply species until the group is better understood.

Several efforts were made to infect the fruit bodies of *Aleurodiscus Oakesii* with the Tremella by introducing the mycelium and the conidia on the young fruit bodies. The Tremella never showed any active growth when thus transferred.

After the Tremella has had opportunity to grow for some time upon the fruit bodies of the host, these latter are often so completely incrusted that one fails to recognize their identity, and the twig appears to be covered merely with a group of little pulvinate plants of the Tremella. Two such fruit bodies are shown in cross section (figs. 10, 11). This leads us to recall other cases of Tremellas associated with different fungi. In 1894 Dangeard (5) described and figured the association of the mycelia of *Dacryomyces deliquescens* and *Tremella* sp., the two finally forming a common hymenium. He speaks of this as a case of symbiosis. Fries (8) described the species *Tremella biparasitica* growing on the stipe of *Nyctalis parasitica*, and *Tremella parasitica*, reported by Schweinitz as growing commonly on *Clavaria gigantea* Schw. in North Carolina. Of this, he uses the significant phrase, "non a Clavaria separabilis."

It is easy to think of the plants commonly placed in the genus Tremellodendron as members of the Thelephoraceae that have Tremellas intimately associated with them. The characters of the hymenium most closely resemble those of the hymenium of Sebacina Tul., which is a genus with decidedly incrusting tendencies. Other genera in this class are Protohydnum and Protomerulius of A. Möller.

However, regardless of what our surmises may be concerning the composite nature of the plants of these genera, we can arrive at definite proof only by producing them through "synthesis" in cultures. In this connection I quote from a personal letter of Professor R. A. Harper:

"There are a number of forms which have been listed under various other genera which are, in my opinion, incrusting if not parasitic members of the Tremellineae. I have always had a suspicion that the Tremellodendron question is mixed up with something of this sort."

## Development and Morphology of the Fruit Body

Pure cultures of the mycelium of both *Aleurodiscus amorphus* and *A. Oakesii* have been obtained by suspending the fruit bodies in test tubes of nutrient agar for a time and allowing the spores to fall upon the agar. The mycelium of *A. amorphus* has never produced fruit bodies in these cultures. Its spores germinate only occasionally in water, and the various decoctions used, including those of Abies bark, have been ineffective for inducing germination. The complete life cycle of the plant has therefore not been traced, nor is it known how infection of the fallen Abies trees takes place. The mycelium of the fungus is found growing through the bark tissues and the cambium. The mycelium remains intercellular. It never enters the phellogenous tissues, and when the other elements of the bark are disintegrated the corky layer remains intact. It is evident as a lightly stained layer, several cells deep, just beneath the epidermis of the bark in figures 1 to 7. In certain areas the mycelium concentrates and forms a cushion-like stroma of pseudoparenchymatous tissue in the bark parenchyma. The hyphae are thicker here than are those that ramify among the elements of the bark, and they branch frequently. As this stroma grows, the surface of the bark is arched upward to form a superficial prominence (figs. 1, 2). There now sets in a strong upward growth of the upper stromal hyphae and the pressure produces a rupture in the bark by which the rapidly elongating hyphae emerge (fig. 2). They branch frequently and continue growth until they attain the form represented in figures 3–5.

The hymenium now begins its formation in the even upper surface. In figure 6 the hymenium is shown in the process of development. The marginal hyphae are longer and more slender from the first, so that under a hand lens they present the appearance of a white hairy margin. Occasionally, in some fruit bodies, these hyphae grow much more rapidly than do the central elements of the fruit body, with the result that the structure is decidedly concave, instead of convex as is typically the case (fig. 7). In some cases, the marginal hyphae have grown so rapidly as to arch over almost completely the young hymenium, so that in sections of these fruit bodies made somewhat tangentially they appear altogether gymnocarp because of the perithecioid form of the structure. This latter method of development the writer attributes to dry conditions of growth, as it is usually encountered on the drier branches of the firs.

In the hymenium the most conspicuous elements are the large basidia with their prominent fusion nuclei. Beside them are the nodulose or moniliform paraphyses and the more slender filiform paraphyses. The basidia keep pace uniformly in their growth so as to present an even, level peripheral surface. The paraphyses project usually about 25 $\mu$ above the general level. When a basidium begins putting out sterigmata it elongates so as to stand some 25 $\mu$ above the general level of the younger basidia. These points are brought out in the photomicrograph (fig. 12), in which one old basidium with sterigmata is shown elongated so as to attain the general level of the paraphyses. In thin sections only two of the four sterigmata are usually seen. To some extent, the age of a basidium can be ascertained from this elevation above the surface. Another check on the degree of advancement of the nuclear divisions is the length of the sterigmata and the size of the primordial spore vesicles. The two divisions of the fusion nucleus are completed when the sterigmata begin to form (fig. 23, Pl. XXXIII). The nest of four daughter nuclei rests for a relatively long time while the sterigmata are elongating and the spores are developing.

The young hyphae and the paraphyses in the hymenium are always binucleate (figs. 17, 18). The nuclei in the primordial basidial cell fuse quite early, even before the basidia have begun to enlarge to any great extent. The fusion nucleus can be easily recognized by its relatively large size, its elongated shape, and especially by the character of the chromatin material (figs. 19, 20). This remains in the form of a spireme throughout the period of the growth of the nucleus until the first nuclear division. It seems that there are many more basidia formed than ever come to sporulation. The upper part of the hymenium is crowded as a result of the large size of the sporulating basidia, and many smaller ones are left below, lacking room for further development.

## Cytoplasmic Structure

The cytoplasm of the hyphae and especially of the basidia presents some very striking appearances when fixed in Flemming's medium solution and stained with haematoxylin. In the young, actively growing hyphae and in the basidia, it consists of a finely granular ground substance in which are embedded larger elements. These larger elements occur in two forms. The most abundant form is that of round or somewhat elongated corpuscles varying in size from minute granules to relatively large bodies reaching 1 $\mu$ in diameter. Less abundant is the second form, which consists of long filaments that may attain a length of 40 $\mu$ or more. Both types of structures present the same appearance under different kinds of staining, and an examination of the preparations leads one to conclude that they are the same kind of substance differing only in form.

The corpuscular forms appear most strikingly in the basidia, for here they are more abundant and often of larger size than in the other elements. They are not distributed uniformly throughout the cytoplasm. The tendency is for them to be most numerous in the upper part of the basidia while in the lower part of the basidia they are usually of somewhat larger size though fewer in number. In many cases they are aggregated about the fusion nucleus of the basidium so as to obscure the detail of the nuclear structures, and this aggregation is usually seen in the upper part of the nucleus so as to give the appearance of a sort of cap (fig. 21). In this connection we are reminded of the description and figures presented by Janssens *et al.* (12) of the mitochondria in the young ascus. They speak of them as forming a cap on one side of the nucleus. In a number of other features the mitochondria described by Janssens agree with the cytoplasmic structures here described. Guilliermond (10), in the first report of the occurrence of mitochondria in fungous tissues, had also described and figured a perinuclear aggregation of these structures in the ascus of Pustularia.

At times the area of more densely aggregated granules is situated higher than the nucleus in the basidium or appears to be moving upward toward the apex of the basidium (fig. 23).

When the basidium puts out sterigmata and forms spores, the granules appear in the cytoplasm of these structures (figs. 23, 28). In fact, they make it difficult to follow the nuclear phenomena here. In the spore at the left in figure 28, for instance, it is difficult to tell whether the spindle-like structure is a nuclear spindle or a group of the corpuscles gathered about the middle of a filament.

The second type of structure, the filamentous form, occurs in both old and young basidia and spores and is occasionally seen in young growing hyphae and paraphyses. These filaments vary considerably in length and thickness, at times attaining a size so large as to appear like a foreign body thrust into the basidium. They are generally straight but may be curved, wavy, or slightly spiral. Occasionally two are seen lying parallel and closely approximated. They almost invariably extend in the direction of the long axes of the hyphae or basidia. The position occupied by one of the three shown in figure 22 is exceptional. Almost every basidium contains from one to four of these filaments. It is seldom that as many as six are encountered in the same basidium.

The filaments are relatively strong, rigid structures. This is easily ascertained by a study of sections that were somewhat broken up in the course of preparation. Here the filaments are often seen projecting out of the end of a broken basidium and maintaining themselves in a rigid position. Several cases, too, were encountered in which a sterigma was broken loose and yet seemed held in place by the unbroken filament (fig. 24).

There is a general tendency for the filaments to be directed toward the apex of the basidium, and when the sterigmata form, the filaments frequently extend into these structures. In fact it is quite common to see a filament extending from the basidium into the sterigma up to its apex.

When the amount of acetic acid in the Flemming's solution is decreased the corpuscular bodies appear even more numerous, although they stand out less definitely than when Flemming's solution is used. This virtually gives Benda's solution used so extensively for mitochondrial fixation. Likewise, Hermann's fluid gives equally good results. With Carnoy's and Zenker's fixatives the cytoplasm presents no structures in the finely granular ground work. These two latter solutions are strong in the amount of acetic acid. What is perhaps the best fixative for preserving the corpuscles and filaments consists of chrom-acetic to which formalin has been added.

This fixative was recommended to the writer by M. l'Abbé Licent who used it with success in the botanical laboratory of the Sorbonne for fixing fungous tissues. His formula is:

| | | |
|---|---|---|
| A. | Chromic acid (2 percent) | 80 parts |
| | Glacial acetic acid | 5 parts |
| B. | Pure formalin (40 percent) | 15 parts |

A and B are mixed only at the time of fixing the material, and a change soon takes place in the fluid reducing the acetic acid and producing green compounds of chromium. The material may be left in the fluid for a few days, which then serves as a chromium mordant.

In general, it appears that the corpuscles and filaments here described are well preserved with osmium fixatives, even though some acetic acid is present. With strong acetic acid fixatives they are not preserved. Chromium compounds give good fixation in the presence of formalin. Once fixed, they are stained equally well with safranin or haematoxylin stains, though they stand out more clearly with the latter. Delafield's, Heidenhain's, and Weigert's haematoxylin methods were used with equal success.

In the old cytoplasm that is growing vacuolar, the granules are larger than in the younger, actively growing regions. Where the fruit bodies are attacked by the parasitic Tremella, the basidia undergo a sort of degeneration and present very large granules. Two such basidia are shown in the photomicrograph (fig. 16), and the basidium shown in figure 26 is drawn from parasitized tissue. If sections are cut of such parasitized plants in formalin (weak solution) with the freezing microtome and mounted in water, the large granules stain the characteristic red with Sudan III, showing that they are of a fatty nature and that in the course of degeneration of the cell the granules undergo a fatty metamorphosis.

In presenting this paper, the writer is more interested in reporting as accurately as possible the observations concerning the cytoplasmic structures in question than in urging any particular interpretation of them. There has been much written about mitochondria in the last decade. Yet we can hardly say that we know what they are. There is no specific technique that brings them out and delimits them from other cell constituents. Of the numerous functions attributed to them much is conjectured and little known for certain. It is difficult to believe that all the structures described by various writers in the cells of animal, fungous, and higher plant tissues are in the same category. The term *mitochondrium* therefore requires to be defined. If every granular or filamentous structure that appears in living cytoplasm and in cytoplasm fixed by various methods is to be called a mitochondrium, then the structures we here describe and figure are mitochondria. In that sense, it would be a generic term under which would fall various types of cytoplasmic structures. If, however, a mitochondrium is defined as a living organ of the cell with a specific function, with an individuality of its own, and with specific staining affinities, then these structures are not mitochondria. Kingsbury (14), in calling attention to the danger of basing morphological generalizations upon special technique without first ascertaining upon what the technique depends, speaks of the difference between these two views as "the issue . . . between a process interpretation of structure as against an elementary particle or material interpretation" (p. 47), and makes out a strong case in favor of the former.

In the cells of the radicle of Pisum the writer has obtained with various so-called mitochondrial fixatives the characteristic granular and rod-like structures commonly described as mitochondria. These can not be said to be identical with the similar structures described above. With Regaud's fixative the former are well brought out, while the latter are only poorly preserved. Flemming's medium solution and the formol-chrom-acetic fixative, on the other hand, fix the former structures (in Pisum) only poorly but preserve the latter well. The structures in the two kinds of tissue have this in common, however, that they are preserved by osmic and chromic fixatives and not with solutions too strong in acetic acid.

In 1902 Maire (17) described fibrils of kinoplasm in the basidia of certain species of Basidiomycetes studied by him, which extend from the daughter nuclei into the sterigmata and are thought to be concerned with the passage of the nuclei into the sterigmata. Fries (9) also makes bare mention of such structures in the basidia of Nidularia in the sentence (p. 155): "Bisweilen sind auch dünne Cytoplasmastränge vorhanden, die von den Kernen aus in die Sterigmaausbuchtungen hinein verliefen." Levine (15) describes and figures these kinoplasmic fibrils in certain species of the Boleti and believes he has determined that they are maintained as a continuous line of connection between the daughter nuclei of the basidium and the centrosomes from the time the former move downward into the basidium and the latter upward into the sterigmata and finally into the young spores themselves. Of their function he says (p. 173): "It is, perhaps, not entirely proven that these fibrillar strands are actively contractile kinoplasmic elements which pull the nuclei into the spores, but the appearances in the Boleti certainly suggest such a conclusion." The same author further says (p. 159): "At this stage I have also found another type of fibrils in the cytoplasm. These latter run irregularly but in the main lengthwise of the basidium. It may be that they are indications of cytoplasmic streaming." It seems likely that these latter fibrils are of the same type as those which I have observed in Aleurodiscus. As for kinoplasmic fibrils connecting the daughter nuclei of the basidium with the centrosomes in the sterigmata and spores, I have never seen them in Aleurodiscus. In the first place I can not establish the presence of centrosomes. In preparations fixed with the osmium and chromium fixatives it would be hopeless to try to find centrosomes among the numerous cytoplasmic granules unless they had well-defined astral rays, and in Carnoy and Zenker preparations no suggestion of centrosomes appears. At first sight, under low magnification, one can easily be deceived into thinking that the filiform structures one sees lead from the nuclei to the sterigmata, since so many of them are found in that region of the basidium. Higher magnifications easily clear up any such error. It might, however, be a timely warning to say that students working with species in which the basidia are small must be on guard against interpreting such structures as are here described as kinoplasmic fibrils connected with the daughter nuclei.

It is a significant fact that Juel (13), who used chrom-platinum-acetic and zinc chloride-acetic-alcohol fixatives in the study of the basidia of nineteen species of the genera Clavaria, Craterellus, and Cantharellus, figures in practically all cases a cytoplasm free from granules, fibrils, or similar structures. Of *Craterellus pistillaris* he says, however (p. 20): "Man sieht oft im Basidienplasma dichtere Plasmastränge, die von jedem Kern gegen die Basidienspitze hinziehen. Fädige Differenzierungen konnte ich in diesen Strängen nicht entdecken."

The writer believes that the granular and rod-like structures bear a relation to the reticular apparatus of Golgi. This characteristic structure, first reported in nerve cells, has since been reported by Golgi as well as other investigators to be present in a variety of different cells. Bensley (1) describes a similar structure in plant cells, and contends that with one type of fixation the vacuolar spaces are shown as separate isolated vacuoles while with a special Golgi technique they appear as a closed net. From the preparations of the writer, it is of course impossible to say in what condition the substance of the cytoplasmic structures in question exists in the living cells of Aleurodiscus. All fixation tends to produce in greater or lesser degree artificial conditions in the cell and it is necessary to interpret these artifacts in order to get at the nature of the substances in question in the living state. From the varying forms that it assumes with different types of fixation and from the fact that with certain fixations it disappears altogether, it seems reasonable for us to conclude that in the living protoplasm the substance exists in the form of a fluid with various substances in solution which have a nourishing function and among which are lipoids in colloidal solution. Where active growth takes place, as in rapidly enlarging basidia or growing sterigmata, the building of new protoplasm makes great demand on these substances and they are therefore present in abundance. They are attracted to points where active growth is taking place, and such attraction may be so strong as to set up definite lines of flowage which, when subjected to a fixative, coagulate in the form of the characteristic rods we have described. Such a manner of thinking of these structures explains their lying lengthwise of the hyphae and their direction towards points of growth. It fails, however, to explain why they should exist in degenerating basidia under the parasitic Tremella (see figs. 16 and 26).

In 1913, Löwschin (16) showed the numerous points of similarity between chondriosomes and myelin forms produced out of lecithin in different salt and albumin solutions under the conditions that lead to the formation of lecithinalbumins. Of the filaments observed, he says (p. 204): "Die langen Fäden, Spermatozoidformen und dergleichen bilden sich, wenn in der umgebenen Flüssigkeit Ströme existieren; die Ursache dieser Ströme mag verschieden sein."

Dangeard (6), in studying both living and fixed cells of Saprolegnia as well as of other plants, finds a canalicular system throughout the cytoplasm which he considers a nourishing apparatus, containing in colloidal solution of greater or lesser density substances of which the chemical nature has not yet been determined, but doubtless related to lipoids. They have the general character of blackening with osmic acid, and possess the same osmotic and elective properties as the metachromatin. They are precipitated in the form of solid granular or filamentous bodies under the influence of absolute alcohol and certain other reagents.

Speaking only for fungous tissue, we may conclude that many of the structures that have been described in the cytoplasm as morphological structures, mitochondria, metachromatic bodies, extranuclear chromatin, and the like, fall into a category of coagulation products resulting from a complex and variable fluid substance in the protoplasm that has the property of reducing osmium tetroxide and chromium salts and that is coagulable into definite structures. The tendency has been in general to interpret these structures from the morphological rather than from the physiological viewpoint.

## Summary

1. *Aleurodiscus amorphus* was collected on twigs and small branches of fallen balsam firs in the Adirondacks. Because of the large cells in the hymenium, it proved to be excellent material for cytological study. It is often parasitized by a Tremella which may completely cover and conceal the fruit bodies of the host. This is compared with other Tremellas that are associated with the fruit bodies of other fungi.

2. The mycelium of the Aleurodiscus grows throughout the intercellular spaces of the bark parenchyma of the twigs and small branches. The fruit body begins its development as a mass of densely interwoven hyphae within the lower tissues of the bark. There is an upward growth of the hyphae, and they emerge through the ruptured corky and epidermal layers. Here they branch and expand into the characteristic fruit body that is typically convex but may be more or less pezizoid in form. The hymenium is characterized by the nodulose paraphyses.

3. In the cytoplasm fixed with osmium and chromium fixatives, large filaments and numerous granules appear, which are thought to be in a class with mitochondria, metachromatic bodies, and other morphological struc-

tures that have been described in the cytoplasm of the fungi. They are interpreted as coagulation products of a fluid vacuolar sap that has lipoid substances in solution. In degeneration under the parasitic Tremella they undergo a fatty metamorphosis.

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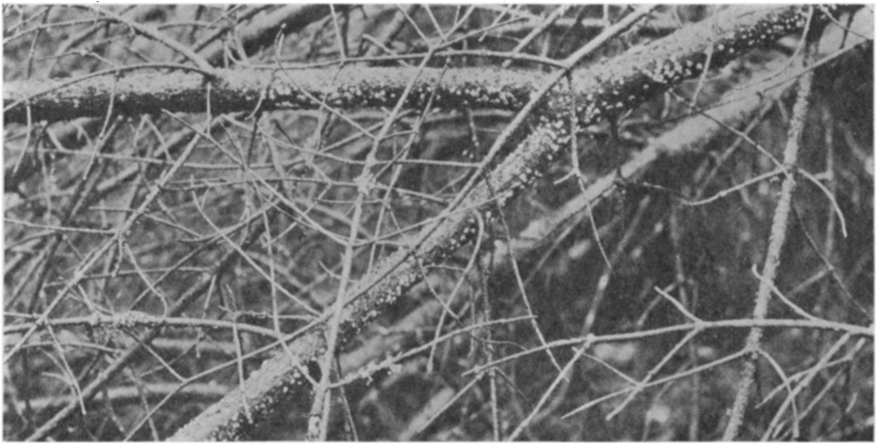
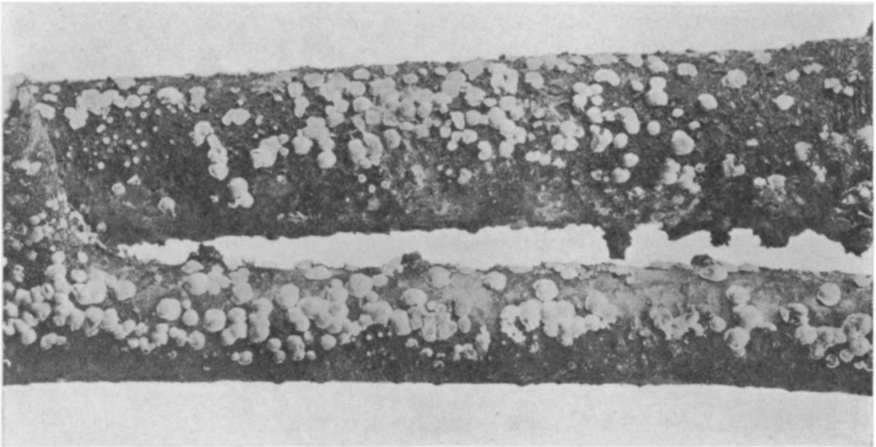
CORNELL UNIVERSITY,
ITHACA, NEW YORK

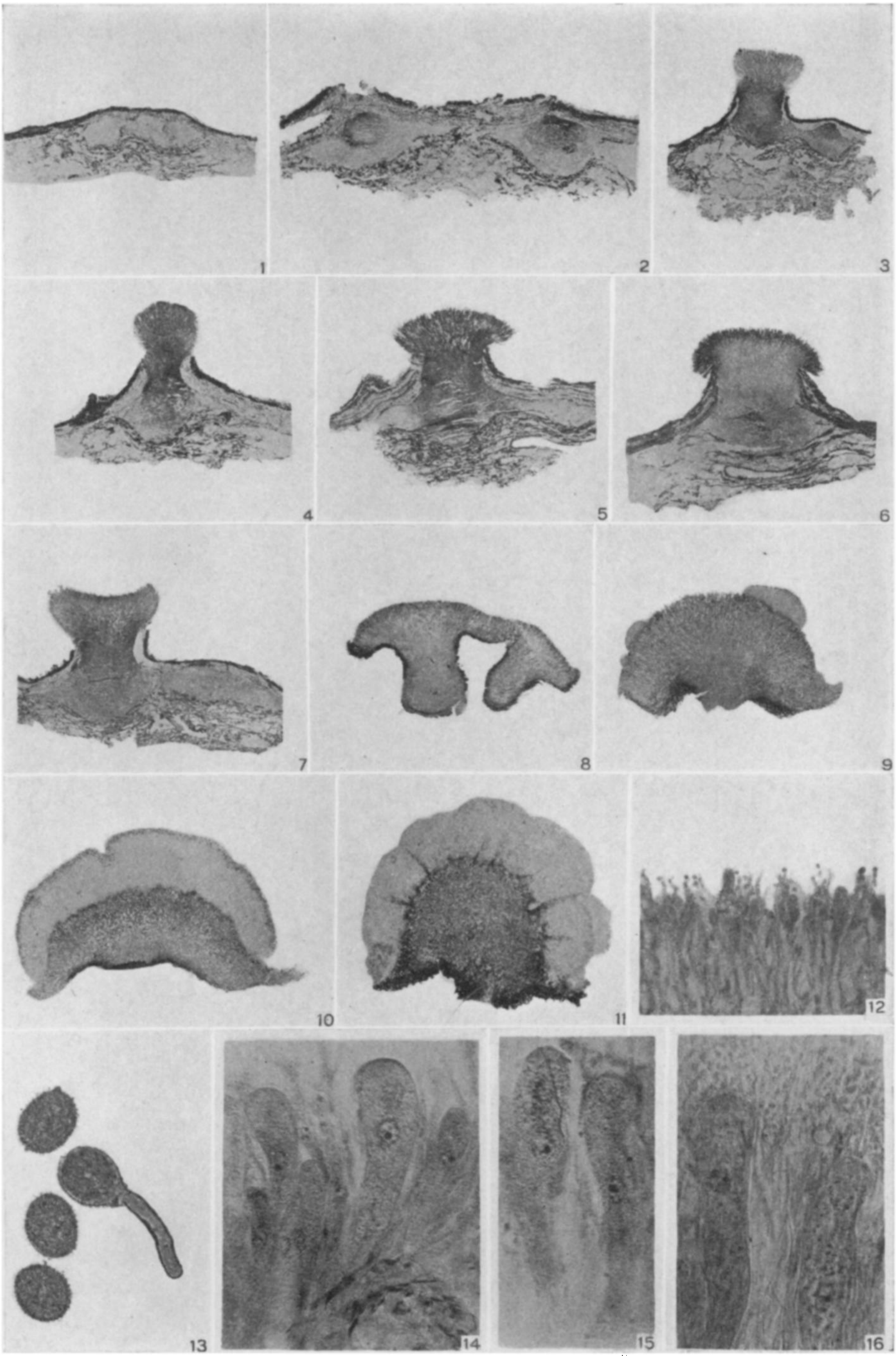
## BIBLIOGRAPHY

1. **Bensley, R. R.** On the nature of the canalicular apparatus of animal cells. Biol. Bull. **19**: 179–194. 3 text figs. 1910.
2. **Berkeley, M. J.** Outlines of British Hymenomycetes. Ann. Nat. Hist. II, **3**: 406. 1849.
3. **Burt, E. A.** Thelephoraceae of North America, IX. Ann. Mo. Bot. Gard. **5**: 180. 1918.
4. **Cooke, M. C.** On *Corticium Oakesii* B. & C. Grevillea **3**: 172. 1875.
5. **Dangeard, P.-A.** Sur un nouveau cas remarquable de symbiose. Botaniste **4**: 182–187. 1 text fig. 1894.
6. **Dangeard, P.-A.** Observations sur le chondriome des Saprolegnia, sa nature, son origine et ses proprietés. Bull. Soc. Mycol. France **32**: 87–96. 1916.
7. **De Bary, A.** Morphologie und Physiologie der Pilze, Flechten und Myxomyceten, pp. 113, 114. Leipzig, 1866.
8. **Fries, E.** Systema mycologicum **2**: 219. 1822. Epicrisis systematis mycologici, p. 590. 1836. 1838.
9. **Fries, R. E.** Über die cytologischen Verhältnisse bei der Sporenbildung von Nidularia. Zeitschr. Bot. **3**: 145–165. 2 pl. 1911.
10. **Guilliermond, A.** Sur les mitochondries des cellules végétales. Comptes Rend. Acad. Sci. Paris **153**: 199. 1911.
11. **Hennings, P.** Hymenomycetineae, in Engler und Prantl, " Die natürlichen Pflanzenfamilien," Teil 1, Abt. 1**, p. 120. Leipzig, 1900.
12. **Janssens, F. A., van de Putte, E., and Helmsmortel, J.** Le chondriome dans les champignons. Cellule **28**: 445–452. Pl. 1, 2. 1913.
13. **Juel, H. O.** Cytologische Pilzstudien I. Die Basidien der Gattungen Cantharellus, Craterellus und Clavaria. Nova Acta Reg. Soc. Scient. Upsaliensis **4**: no. 6, pp. 1–40. 3 pl. 1916.
14. **Kingsbury, B. F.** Cytoplasmic fixation. Anat. Rec. **6**: 47. 1912.
15. **Levine, M.** Studies in the cytology of the Hymenomycetes, especially the Boleti. Bull. Torrey Club **40**: 137–181. Pl. 4–8. 1913.
16. **Löwschin, A. M.** Myelinformen und Chondriosomen. Ber. Deutsch. Bot. Ges. **31**: 203–209. 1913.
17. **Maire, R.** Recherches cytologiques et taxonomiques sur les Basidiomycètes. Bull. Soc. Mycol. **18**: 1–209. 8 pl. 1902.
18. **Morgan, A. P.** The mycologic flora of the Miami Valley. Journ. Cincinnati Soc. Nat. Hist. Jan., 1888, p. 199.
19. **Peirce, G. J.** Notes on *Corticium Oakesii* B. & C., and *Michenera Artocreas* B. & C. Bull. Torrey Club **17**: 301–310. 1 pl. 1890.





STORK: BIOLOGY AND STRUCTURE OF ALEURODISCUS.

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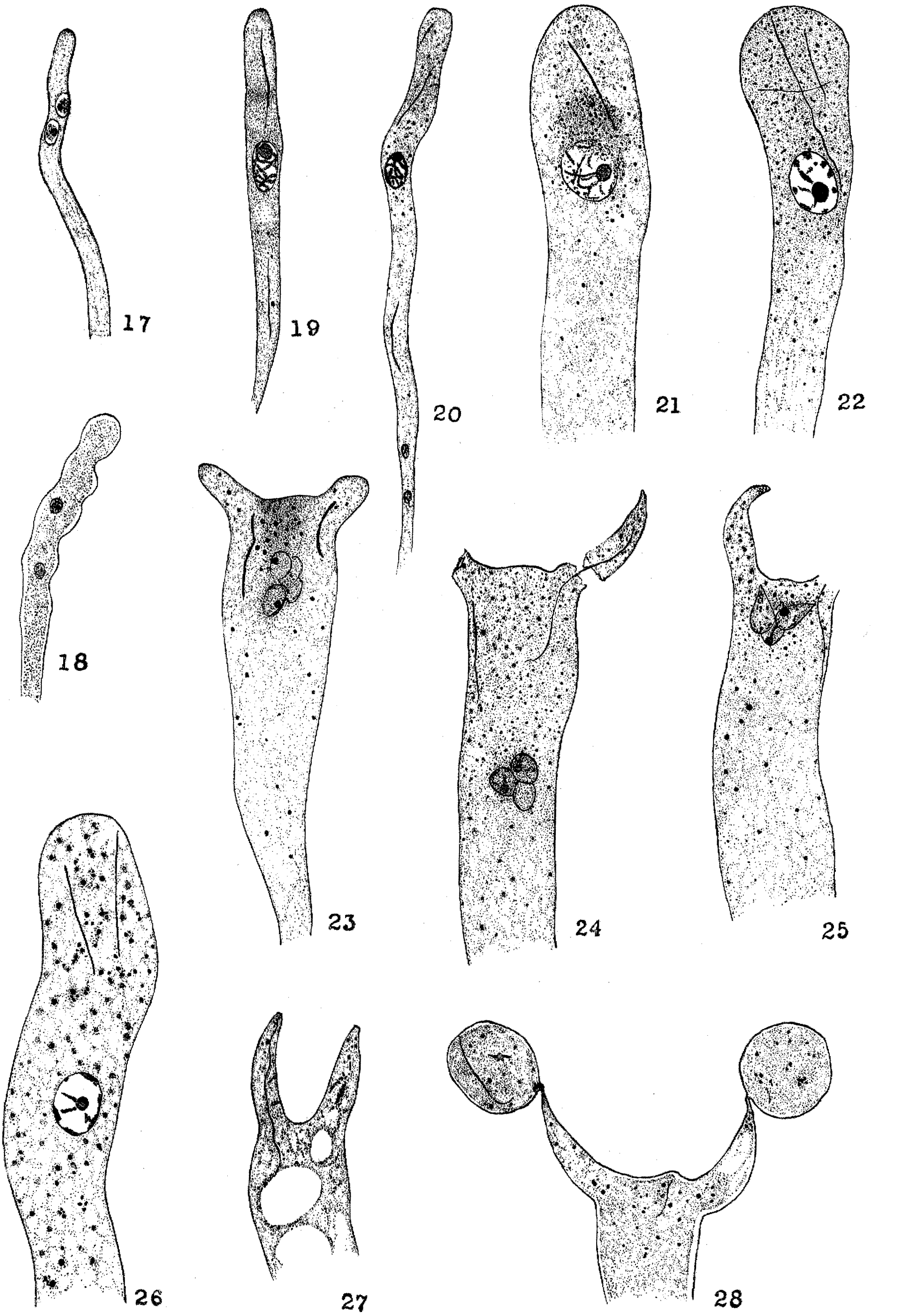


STORK: BIOLOGY AND STRUCTURE OF ALEURODISCUS.

## EXPLANATION OF PLATES

### Plate XXXI

Upper figure: *Aleurodiscus amorphus* on Abies twigs. ¼ natural size.
Middle: Same, natural size.
Lower: *Aleurodiscus Oakesii* on bark of living Ostrya. Natural size.

### Plate XXXII

Figures 1–11, × 12. Figure 12, × 84. Figure 13, × 440. Figures 14–16, × 390.

Fig. 1. Section of bark of Abies with a stroma of pseudoparenchymatous tissue of *Aleurodiscus amorphus*, the primordium of a fruit body.

Fig. 2. Two similar primordia somewhat further advanced.

Fig. 3. A fruit body that has broken through the outer layers of bark and a smaller one about to emerge by its side.

Figs. 4–6. Further development of the same. In the fruit body shown in figure 6 the hymenium has begun to develop.

Fig. 7. Pezizoid type of fruit body. The numerous thin white hyphae on its sides and margin give it a tomentose appearance.

Fig. 8. Two confluent fruit bodies.

Fig. 9. Fruit body with three stromata of *Tremella* sp. growing upon it.

Fig. 10. Later stage of a similar fruit body, the Tremella having entirely covered the host. The hymenial layer of globose basidia appears as a border of black dots on the upper surface.

Fig. 11. Similar to preceding.

Fig. 12. Section of hymenium of *Aleurodiscus amorphus* showing basidia and paraphyses. One older basidium is seen with two sterigmata in the section.

Fig. 13. Germination of basidiospore.

Fig. 14. Basidia and paraphyses. Flemming fixation. The granules are evident in the basidia, but no filaments lie in the plane of focus.

Fig. 15. Basidia. Formol-chrom-acetic fixation. Granules and one filament visible.

Fig. 16. Two basidia in a hymenium, above which is seen the tissue of the parasitic Tremella. Notice the larger corpuscles in the basidia.

### Plate XXXIII

(All figures × 880)

Fig. 17. Filiform paraphysis.

Fig. 18. Nodulose paraphysis.

Fig. 19. Young basidium showing granules and filaments.

Fig. 20. Basidium in lower part of hymenium, perhaps old but crowded for room and unable to elongate. No cross wall is here present.

Fig. 21. Growing basidium showing cap of granules and one filament above the fusion nucleus.

Fig. 22. Several filaments visible, one occupying an exceptional horizontal position.

Fig. 23. Aggregation of granules apparently proceeding to apex of basidium. Filaments tending toward the growing sterigmata.

Fig. 24. Sterigma broken loose from the basidium in the course of preparation, the filament remaining intact.

Fig. 25. Beaked daughter nuclei ready to proceed into sterigmata. No fibrils are seen attached to them.

Fig. 26. Degenerating basidium from hymenium parasitized by *Tremella* sp. The large corpuscles stain with Sudan III.

Fig. 27. Old vacuolate basidium after sporulation.

Fig. 28. Spores in process of formation. The one at the left shows a filament and what is probably a nuclear spindle.